Nests and Immature Stages of the Bee
Paratetrapedia swainsonae
(Hymenoptera: Anthophoridae)

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ABSTRACT

Nests, mature larvae, pupae, and flight behavior of the Jamaican bee, *Paratetrapedia swainsonae,* are described. In spite of the tropical climate, the population is well synchronized, one generation per year, and adult activity is limited to little over two months per year. This species nests in large aggregations in vertical banks of soft earth. There is no evidence of burrow use by more than one female at a time, but reuse is common. Cells are symmetrical, or nearly so, and lined. Mature larvae construct silk cocoons and most or all of their defecation occurs after cocoon construction. Probable mating flight behavior of males is away from the nesting sites and around plants with moderate-size (rather than large) leaves. No features were discovered that indicate that *Paratetrapedia* should be removed from the Exomalopsini.

INTRODUCTION

The tropical American genus *Paratetrapedia* is usually placed in the anthophorine tribe Exomalopsini (Michener and Moure, 1957). It is, however, quite different from *Exomalopsis* and further study of its characters is needed to determine whether it is properly placed in the same tribe with that genus. Descriptions of nests and immature stages can contribute to such an inquiry. Nests of *Paratetrapedia* in earthen banks have been reported only for *P. (Trigonopedia) oligotricha* (Moure) (Michener and Lange, 1958; Michener et al., 1958) and *P. (Xanthopedia) swainsonae* (Cockerell) (Raw, 1975, 1984). The only nests in soil known for the genus are those of these two species, whose subgenera are small; nests of the common large subgenera *Lophopedia* and *Paratetrapedia*

s. str. are unknown except that *P. (P.) gigantea* (Schrottky) nested in a fallen dead tree trunk (Oliveira, 1962) and *P. (P.) lugubris* nested in artificial holes in wood (a trapnest designed for *Megachile*) (R. W. Brooks *in* Rozen, 1984). Nest and cell structures have not been described for these species. Larvae have been described for *P. gigantea* by Oliveira (1962). The objective of the present study is to offer more information on nests, larvae, and pupae of *P. swainsonae,* not only to add to the biological data available on Neotropical bees but also to provide information for decisions as to the tribal relationships of the genus.

Paratetrapedia swainsonae was described from Bath, St. Thomas Parish, Jamaica (Cockerell, 1909). Raw (1975, 1984) recorded it from near Seaforth, St. Thomas Parish, and from Strong Hill and Irish Town, St. Andrew Parish. All these localities are on the south side of the Blue Mountains at altitudes of 300 to 700 m. As indicated above, this species is a member of the subgenus *Xanthopedia,* hitherto not recognized north of Panama. It is closely related to *T. (X.) globosula* (Friese) as identified by Michener (1954) and others, differing principally by the reduction or absence of black areas on the scutum. It is possible that *P. swainsonae* and *globosula* are conspecific.

Throughout the rest of this paper, the two references by Raw are indicated by the single word Raw.

JGR prepared the descriptions of immature stages and did much of the analysis of cocoon structure. Both authors analyzed cells. CDM did the fieldwork including descriptions of nest sites, burrows, flight behavior, and analysis of Raw's earlier study of this species.

THE NESTING SITE AND FOOD SOURCES

Our material was obtained by CDM at and near Irish Town, Jamaica, at some of the same nest aggregations that were studied by Raw. This locality, about 10 km northeast of Kingston, has a considerable human population and many introduced trees, flowers, and crop plants. There are fragments of native vegetation especially in deep stream valleys, and there is an intermixture of native species elsewhere.

Nests were in aggregations in vertical roadside banks of pale soil that was soft and friable, commonly with a considerable sand content. Surfaces were dry and dusty in early June but dried algae indicated humidity at other seasons. Larger vegetation was nearly absent from the banks studied by CDM. The six aggregations studied by Raw faced north, northwest, northeast, and south; the principal one studied by CDM faced west, southwest, to almost south. This aggregation, on Bermuda Road, was about 5 m long and 1 to 1.5 m high, in the upper part of a vertical bank about 2.5 m high. The uppermost, root-filled part of the bank overhung and during much of the day shaded the rest of the bank. Three small aggregations (50–60 nests each in a bank facing north along Strawberry Hill Road, ranging from nearly road level to about 1.3 m above it) were also protected from above, in this case by overhanging roots of a large mango tree. Raw did not comment on protection of nest sites, but the tendency seems to be to nest in soil so soft that it would be severely eroded by rain if not protected from above.

All aggregations seen by CDM seemed to have been long established, as indicated by the presence of vacated cells in the soil. Such cells or remnants of cells and burrows were visible at the surface, showing that considerable erosion had occurred during the occupancy of the banks by bees. In spite of the density of nests, CDM found no parasites or other natural enemies.

Nest burrows were dense, neighbors often less than 2 cm apart, old and recent ones being intermixed. Other aggregations along the Bermuda Road and elsewhere were mostly less dense, some consisting largely of old burrows. Raw reported that 598 adults emerged from a block of bank soil 25 × 25 cm and deep enough to include the deepest cells. His table showed that this represented approximately 50 percent survival of the 1187 eggs originally in the block (see section on Seasonality below).

Food sources of the adults are little known. CDM saw males occasionally stopping briefly, apparently for nectar, on flowers of *Verbena* sp. (Verbenaceae), a purplish compos-
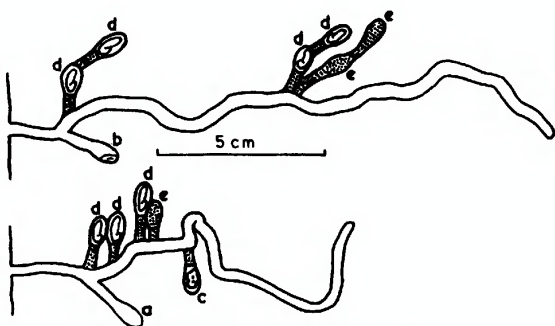
Fig. 1. Nests of *Paratetrapedia swainsonae* viewed from above. **a,** newly constructed empty cell; **b,** cell being provisioned; **c,** large larva; **d,** prepupae (quiescent larvae); **e,** earth-filled cells presumably used the previous year. (Modified from Raw, 1975, with permission)
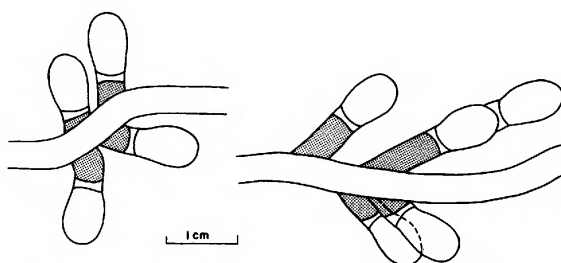

Fig. 2. Portions of two nests of *Paratetrapedia swainsonae* viewed from above showing groups of cells, all of which contained prepupae, pupae, or young adults still in cocoons on June 3, 1985. Stippling represents earth-filled lateral burrows. Nest entrances were to the left.

ite, *Lantana camara* (Verbenaceae), and an unidentified small native tree with minute whitish flowers. Raw reported females foraging at flowers of *Bidens pilosa* (Compositae), *Oreopanax capitatus* (Araliaceae), and *Cyrilla racemiflora* (Cyrillaceae), but did not specify whether this was for pollen, nectar, or both. At the time of CDM's study, no pollen collecting was occurring and all scopae were clean. Many if not all *Paratetrapedia* species are oil collectors (Vogel, 1971, 1974), and both CDM and Raw examined flowering Malpighiaceae, the oil source for some *Paratetrapedia,* to see if *P. swainsonae* might be collecting oil from the flowers. None was seen on or near Malpighiaceae, however. The scopa of one female of the closely related *P. globosula* from Panama carried abundant pollen of a single species, probably *Byrsonima crassifolia,* a malpighiaceous tree (identified by David W. Roubik).

NEST ARCHITECTURE

BURROWS: In the dry friable soil, with nests densely spaced, CDM had difficulty in excavating and understanding individual nests. The burrows are more or less horizontal but irregular, often with numerous and sometimes sharp curves in any direction, as illustrated by Raw (fig. 1). They are never filled with soil and lack plugs and septa. They are 3 mm in diameter, irregularly enlarged to 4 mm near entrances where washing or blowing may have influenced the diameter. Entrances

are mere openings, often somewhat irregular, with no turrets or other elaboration. There was no evidence that they are ever closed by the bees. Burrow walls are not especially smooth or lined by the bees. Burrows commonly (but not always) extend deeper than any cells, to depths of about 12 cm; Raw illustrated one that must have attained a depth of about 17 cm. There was no evidence that more than one bee works in a burrow at the same time. Old burrows are reused, however, as shown by occupied cells attached to the same burrows with old, earth-filled cells in illustrations by Raw. Independently (before he saw Raw's work), CDM reached the same conclusion after finding fresh cells (ready to receive pollen) built off burrows connected to old, earth-filled cells. Moreover, he never found a burrow cutting through an old cell. This suggests that the burrows tend to remain in place as cells are constructed around them in succeeding years. Considering the density of cells and nests, burrows should often cut through old cells if newly constructed each year.

Lateral burrows of the same diameter as the main burrow and 2–10 mm long lead to the cells. Except when a cell is being prepared and provisioned, these burrows are earth-filled (as shown also by Raw), making them hard to follow in the loose, dry matrix. Lateral burrows are usually more or less horizontal; their angles relative to the main burrow are highly variable. Frequently lateral burrows are clustered, resulting in clumps of cells (fig. 2), but cells may be isolated as in figure 1. Most lateral burrows end in single
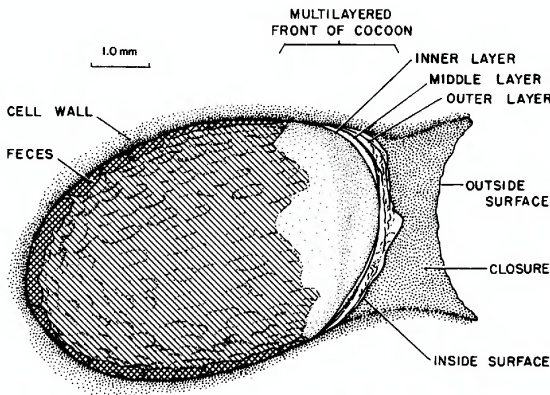
Fig. 3. Cocoon and cell of *Paratetrapedia swainsonae*, cut longitudinally. For explanation, see text.

cells that more or less extend the axis of the laterals, but some end in two or rarely three serially arranged cells. They may be widely separated by earth-filled sections (several mm long) of lateral burrow as in Raw's figures. However, in most cases seen by CDM the wall between cells in a series was less than 1 mm thick.

CELLS: Cells (fig. 3) do not usually come out of the matrix intact but do have walls (0.2–0.5 mm thick) around them of firm soil, pieces of which can be separated from the matrix. When there is a cocoon, the cell hangs together better and is more likely to remain intact as the surrounding matrix is broken up. The wall is harder, darker, and of slightly finer earth than the substrate, so must be constructed by the bee, but there is no sharp demarcation between it and the substrate (as

is found, for example, in *Melitoma* whose cells are easy to extract intact from the substrate). The wall extends into the lateral burrow at least as far as the outer surface of the cell closure.

New cells are sometimes constructed cutting into old, earth-filled cells. In two cases JGR found a new cell coinciding with an old one, the old and new linings separated by a layer of soil 0.1 mm thick. Such observations are further evidence that the cell linings are constructed by the bees.

At Bermuda Road, cell depths (from the surface of the bank) ranged from 2 to 8 cm. (Raw's illustrations indicate 2–11 cm.) There was no evidence that cells near the surface were in such a position because of erosion after they were first constructed. One newly constructed cell was at a depth of only 4.5 cm.

We have two sets of measurements of cells (table 1), one made by JGR on cells taken to New York, the other by CDM on cells examined in the Blue Mountain Field Station of B. E. Freeman. While generally in agreement, these measurements are given independently since there was no effort to standardize methods.

The principal axes of cells are somewhat variable, usually nearly horizontal, sometimes sloping downward toward the rear but never approaching vertical. Cell symmetry seems variable, and we are uncertain whether cells are typically symmetrical around their long axes. The inner ends are evenly rounded, but in some cases the plane of the cell closure was not at right angles to the long axis. Prob-

TABLE 1

Measurements (mm) of Cells of *Paratetrapedia swainsonae* Made Independently by the Two Authors

	JGR			CDM		
	$\bar{x}$	Range	N	$\bar{x}$	Range	N
Inside cell diameter	4.5	4.3–4.7	7	4.5	4.3–4.7	3
Cell length	6.2	6.0–6.3	5	8.5[a]	8.4–8.5[a]	3
Cell closure diameter (inside)	3.2	3.0–3.3	8	3.2[b]	3.0–3.3[b]	3
Cell closure diameter (outside)	3.7	3.5–4.0	6			
Thickness of closure (at margin)	2.0	1.7–2.5	5	2.0		1
Thickness of closure (at center)	0.7		2	0.7		3
Cocoon diameter				4.4	4.3–4.5	4
Cocoon length				6.4	6.0–6.5	3

[a] To where lining fades away in lateral burrow; based on fresh cells without closures.

[b] Measured at narrowest point of cell entrance, not at inside or outside surface of closure.

ably this occurs when the main axis of the lateral burrow is not the same as that of the cell.

The inner surface of the cell is smooth, with only faint irregularities imposed by hard inclusions in the cell wall. It is coated evenly with a shining, dark brown lining approximately 8 microns thick. Its inner surface appears dark and faintly shiny in completely dried specimens, and blackish in old cells in the field. The lining was waterproof when tested with water droplets and when heated on a hotplate to 700°F, it darkened but did not melt. The surface of the lateral burrow (like the main burrow) is much more uneven than the cell wall, and the cell lining continues into the lateral burrow at least as far as the outer face of the cell closure before fading away.

The cell closure, made of hard soil like the cell lining, is concave and with a spiral pattern on the inside and concave, uneven, but nonspiraled on the outside. In contrast to that of other exomalopsines, the inner surface of the closure is visibly coated with a dark lining identical in color and shininess to the cell lining. The spiral inner surface consists of three to four coils, the central ones tending to be more recessed than the outer ones; as a consequence the central coils appear almost pitlike. This pit does not penetrate to the outer surface of the closure, but may do so at the time when the lining of the closure is applied. Both inner and outer surfaces are water retardant; in some specimens they seemed to absorb water somewhat faster than the cell lining, but in others they were waterproof like the cell lining. When pressed with forceps against the microscope stage, closures abruptly fractured revealing a glistening-as-if-wet fractured surface. Soil particles within the closure are moderately coarse and contain interstices that may play a role in gas exchange. However, the inner surface of the closure reveals no interstices because of the thick lining, although the surface texture of the closure is coarser than that of the cell wall.

In several vacated cells the emerging bee had chewed a hole through the anterolateral side of the cocoon and cell wall rather than through the cell closure. In other cases the cell closure appeared to have been destroyed by an emerging bee. Further investigation

might reveal whether these bees often egress through the side into the soft substrate rather than through the front of the cell.

COCOONS AND LARVAL DEFECATION: All cells without cocoons lack feces; therefore this species must regularly spin cocoons. They are spun before larval defecation, or at least before defecation is completed, as all cocoons contain feces on the inside of the fabric. JGR, carefully examining about 20 cells with cocoons, found no indication of fecal material either imbedded in the fabric or deposited between the cell wall and the fabric. Among all exomalopsines, this situation has been reported before only for *Tapinotaspis caerulea* (Friese) (Claude-Joseph, 1926). It suggests that defecation must commence well after provisions are consumed, an unusual occurrence in the exomalopsines (Rozen, 1984), which tend to start defecation at the beginning of the last larval stadium and well before the food has been depleted. Cocoons are uniform in that they are constructed in the same way from the same amount of silk. The rear three-quarters of the cocoon consists of a single layer of fine silk fiber matted into a soft tan fabric that resembles in texture, but is thinner and softer than, brown wrapping paper. At the front of the cocoon, against the cell closure, the fabric forms a number of separate, nearly concentric sheets. The exact number seemed variable from one cocoon to the next, and perhaps some sheets do not extend completely across the front of a cocoon. The outermost sheet, next to the spiral cell closure, is distinctive in that its central part (near the center of the closure) consists of a mass of loosely curled silk strands rather than a flat sheet. Toward the periphery, this layer is more sheetlike, and strands of curly silk run from it to the next layer inside the cocoon. Beneath this outer, fuzzy layer, the thickest sheet of silk curves across the front of the cocoon. (In some instances there was a suggestion of a fine fenestrated layer of fabric between these two.) This thickest (middle) layer is nearly identical in thickness and texture to the fabric of the rear part of the cocoon. The innermost layer is similar to, but thinner than, the middle one and curves from the wall to the center of the cocoon front where it contacts and perhaps fuses with the thick middle one. In some cases one or two

layers could be identified between the innermost and the middle layers. The greatest thickness of all layers combined was nearly 0.5 mm, in contrast to the fabric thickness elsewhere that was less than 0.1 mm. The front end of the cocoon had no opening such as a macropyle (Rozen and Jacobson, 1980).

Feces, as noted by JGR, are plastered over all surfaces of the rear two-thirds to three-fourths of the cocoon (fig. 3) as dark brown, elongate pellets or streaks, generally paralleling the longitudinal axis of the cocoon. At the rear of the cell they tend to be multidirectional. Adhering to the cocoon's inner surface, they form a coating 0.3–0.4 mm thick. In none of the cocoons studied by JGR was fecal material found on the multilayered front part of the cocoon, nor was there fecal material between any of the layers.

CDM, however, examining large numbers of cells and cocoons in the field and in the Blue Mountain Field Station of B. E. Freeman, found occasional exceptions to JGR's detailed description. In some cases feces covered the entire inner surface of the cocoon except the closure area to a depth of 0.1 to 0.2 mm. In one cell the feces were limited to the posterior half of the cocoon. In another cell there was a thin fecal layer on the entire inner surface of the cocoon including the closure side. In a few cases there were feces (or uneaten pollen?) on the outside of the cap of the cocoon against the cell closure. One cocoon consisted of two layers that could be pulled apart at the sides of the cocoon; feces inside were found only at the posterior end, but there were also feces scattered on the outside of the cocoon against the cell lining. In all cases the quantities of silk and fecal material did not seem unusual. Developmental irregularities might well result in variations in relative times of defecation and cocoon spinning.

PROVISIONS

We have nothing to add to Raw's account indicating that pollen is brushed into the cell until it is about half provisioned, after which the pollen is molded into a slightly flattened sphere. After additional loads of pollen are provided, the food mass is completed. The egg is 1.4 mm long, gently curved, and in contact with the top of the food mass at both ends. Raw's illustration showed a slight depression of the upper surface of the pollen mass beneath the egg; otherwise it is a flattened sphere.

SEASONALITY

Raw indicated that there is only one generation per year, the adults being active in June and July. Overwintering is as fully developed, quiescent larvae in cocoons, with pupal development occurring shortly before maturation. Emergence is protandrous; males emerged from a sample of cells from May 26 until June 8 with a peak on May 27, females emerged on May 28 to June 9 with a peak on June 6. In a block of soil nearly 50 percent of the prepupae remained in that stage through the summer but died before the following June, perhaps because the block became too dry. CDM noted that on June 3, 1985, in 52 cells along Bermuda Road, there were 50 pupae and adults still in cocoons, and only two prepupae (quiescent larvae). The youngest pupae were all becoming pigmented; thus there was a considerable developmental gap between the pupae and the two quiescent prepupae, which might have lived until the following summer.

CDM's field study was June 2 to 9, 1985. At Strawberry Hill Road no adults were seen but the old nest entrances showed nest aggregation sites. Excavation revealed pupae and adults still in cocoons. At the Bermuda Road site and in Irish Town proper, adults were already flying in numbers. All were unworn (no mandibular or wing wear), and males predominated (see next section). No females were carrying pollen; scopae were clean. No loose dirt was seen pushed out of or fallen from nest entrances, but a few newly made but empty cells had already been constructed, no more than one per nest, and most nests contained none. There were no provisioned cells or feeding larvae. A sample of cells still containing intact cocoons revealed the following: 2 prepupae (quiescent larvae), 20 pupae, 28 adults (in cocoons), 2 dead adults (in cocoons). All these observations are consistent with a well-synchronized population beginning its seasonal flight period. Specimens in the Institute of Jamaica were col-

lected on May 23 and 27, 1972 (males only) and June 23, 1963 (5 females, 1 male). Dr. Brian Freeman wrote that he collected about the Irish Town nest sites in 1985 and that *Paratetrapedia* stopped flying about mid-August. These data support Raw's statement about seasonality.

FLIGHT BEHAVIOR

Foraging had not yet begun during CDM's study. Nonetheless there was much flight activity, especially by males. A sample of 50 bees taken flying within 10 cm of the bank at Bermuda Road (8:30–11:30 A.M.) was all females. They frequently entered holes, and often flew about as though seeking a nest. A few males flew farther from the bank and sometimes, especially in late morning, were seen entering holes. Apparently mating activity is not at the nest sites.

Males were common in flight 2 to 20 m from the nest site or at even greater distances. They visited flowers occasionally, as noted above. Their main activity, however, was rapid zig-zag flight around foliage and sometimes flowers. These flights were concentrated around plants with moderate size leaves, such as mango, hibiscus, bougainvillaea, and poinsettia. They were seen along branches of a leafy tree to a height of 5 m. In most places the bees were not dense; usually a single bee could be seen flying about any meter-long leafy branch. Around one small tree, however, hundreds were in flight. Flight began as early as 7:30 A.M., but there was much more activity after 8:30; it continued through the morning and at a reduced level at least to mid-afternoon (often interrupted by cloudy or rainy weather).

A reasonable assumption is that this intense activity is related to mating. There was no indication of interaction among flying males. They did not chase one another, defend territories, etc. Once a possible mating was seen; one bee pounced on another for about 10 seconds. One sample of 28 bees swept from vegetation contained a single female.

Vegetation with large or long and slender leaves seemingly was not attractive to the male bees. None was seen in flight about leaves of banana, *Heliconia, Yucca,* or tall grass and cane, even when in the midst of attractive plants.

POSTDEFECATING LARVAE
Figures 4–12

Oliveira (1962) described and illustrated the postdefecating larva of *Paratetrapedia gigantea* (Schrottky). Although her description closely parallels ours of *P. swainsonae,* incongruities seem to exist between her description and drawings. For example, she stated that the labium projected farther than the maxillae and that the prementum was separated from the postmentum. However, the illustrations depicted a recessed labium with only a suggestion of a subdivided prementum and postmentum. This and the fact that the salivary lips were not shown as being pronounced might imply that the illustrated larva was a penultimate instar (although an alternative explanation might be that the species does not spin a cocoon). Because of these apparent discrepancies, we find it difficult to interpret her presentation in the following account.

The mature larva shares many features with *Exomalopsis chionura* Cockerell (Rozen, 1957) and *E. nitens* Cockerell, specimens of which have been examined by JGR. It can be distinguished from these two by the wider salivary lips, more elongate antennal papillae, and the ventral apical mandibular tooth being longer than the dorsal one. Nonetheless, the general shape of head and body, the form of the mandible, and numerous other features are similar to those of *Exomalopsis* and not too different from those of various melitomines and eucerines.

In the following description, comparisons with *Exomalopsis* refer to only the two species mentioned, both of which spin cocoons and which therefore have produced labiomaxillary regions. Some species of *Exomalopsis* have recessed labiomaxillary regions and do not produce cocoons.

HEAD (figs. 5, 6): Integument of head capsule with scattered short sensilla that are not obviously setaform; sensilla of mouthparts somewhat larger with some distinct short setae evident on apex of labrum, outer surface of mandible and apices of maxilla and labium. Integument weakly pigmented, the fol-
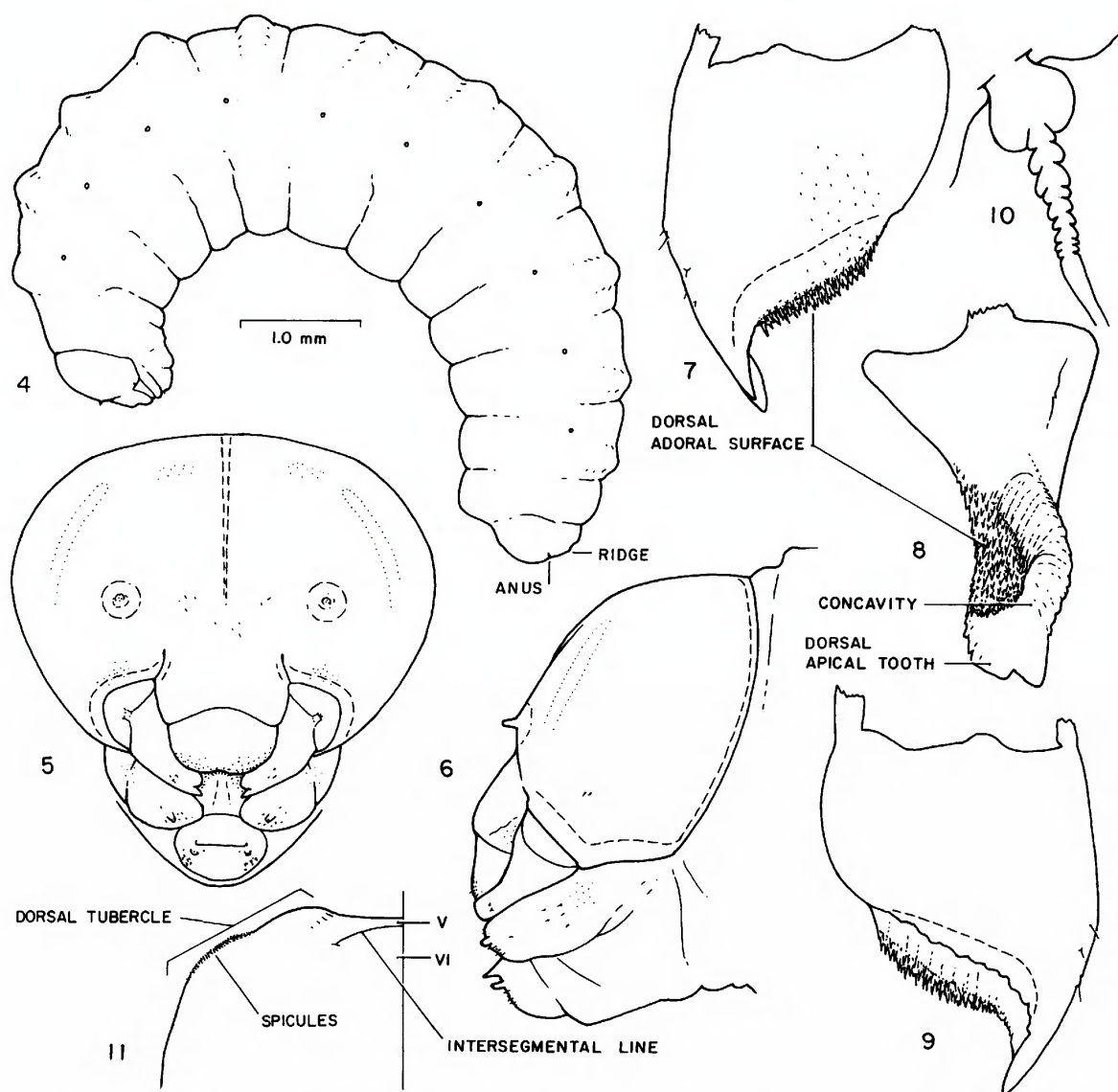
Figs. 4–11.   Mature larva (prepupa) of *Paratetrapedia swainsonae*. **4.** Lateral view. **5, 6.** Head, frontal and lateral views. **7-9.** Right mandible, dorsal, inner, and ventral views. **10.** Spiracle, side view. **11.** Abdominal segment VI, rear view, showing transverse dorsal tubercle with spiculated area on outer part. Scale refers to figure 4.

lowing somewhat darker: antenna, mandibular articulations, apex of labium, apex of maxilla, posterior tentorial pit, dorsal extremity of premental sclerite, and salivary lips; only mandibular apex darkly pigmented.

Head size (fig. 4) normal in comparison to body; head capsule about as wide as long. Tentorium strongly developed, possessing dorsal arms; anterior pit moderately low on face, not immediately adjacent to mandibu-

lar precoila; posterior tentorial pit normal in position, at junction of posterior thickening of head capsule and hypostomal ridge; posterior thickening of head capsule well developed, only slightly curving forward medially as seen in dorsal view; posterior boundary of head capsule normal, as defined by posterior thickening of head capsule; median longitudinal thickening of head capsule well developed above, gradually tapering and disap-

pearing at about level of antennae; hypostomal ridge well developed, without dorsal ramus; ridge moderate in length, forming obtuse but distinct angle with posterior thickening of head capsule; pleurostomal ridge well developed; epistomal ridge evident only between mandibular precoila and anterior tentorial pit; epistomal depression between pits inconspicuous, not arching upward. Parietal bands inconspicuous but present. Antennal prominences weakly developed as in *Exomalopsis*; antennal disk moderate in size; antennal papilla moderately large, tapering apically and more elongate than that of *Exomalopsis,* longer than basal diameter, and bearing three sensilla. Vertex evenly rounded, as seen from side, without unusual projections or tubercles; clypeus narrow in frontal view; frontoclypeal area, in lateral view, normal, not produced beyond labrum. Labrum, in lateral view, not strongly projecting beyond clypeus; labral sclerite not evident; labral tubercles absent as in *Exomalopsis*; labral apex, in frontal view, only faintly emarginate; sensilla-bearing swellings on labral apex vaguely evident (these are probably not homologues of the forward-projecting labral tubercles found in many Nomadinae and Panurginae or of the downward-projecting lateral tubercles of Eucerini); epipharynx slightly produced along median line, with conspicuous, long, setalike spicules on either side.

Mandibles (figs. 7–9) moderately elongate and moderately robust; dorsal mandibular spiculation present but weak; outer surface of mandible without conspicuous seta-bearing tubercle, but with some setae on small tubercles; mandibular apex strongly bifid; ventral tooth projecting somewhat farther than dorsal tooth in adoral view in contrast to *Exomalopsis* in which the dorsal tooth is longer (in *Paratetrapedia gigantea,* Oliveira, 1962, depicted and described the dorsal tooth as larger and longer than the ventral one); large tooth on dorsal apical edge near cusp absent; apical portion of mandible in adoral view somewhat parallel-sided, more robust than in *Exomalopsis,* neither attenuate, nor tapering; mandibular cusp[3] rounded, without conspicuous sharp cuspal projection; dorsal adoral surface of mandible sharply projecting and heavily dentate in contrast to deep apical

concavity between projecting adoral surface and ventral apical edge; mandibular apical concavity extremely well developed (much more so than in *Exomalopsis*), strongly scooplike because of projecting dentate dorsal adoral surface and projecting ventral apical edge (this edge weakly defined in *Exomalopsis*); spines on apical concavity absent, but integument with indistinct curved striae leading to dorsal adoral surface; ventral apical edge jagged (smooth in *Exomalopsis*). Labiomaxillary region (fig. 12) produced, as generally characteristic of cocoon-spinning larvae; labium and maxilla not extensively fused and projecting equally. Maxillary apex produced somewhat mesially; sclerotized cardo only faintly visible, as in *Exomalopsis*; stipital sclerite (see Remarks) distinct, somewhat pigmented; articulating arm of stipital sclerite (for definition, see Remarks) distinct, somewhat pigmented, articulating with pigmented dorsal extremities of premental sclerite; maxillary palpus moderately small, longer than basal diameter but considerably shorter than in *Exomalopsis,* arising apically on maxilla; galea absent. Labium divided into prementum and postmentum; premental sclerite not defined except darkly pigmented near articulating arms of stipital sclerite; labial palpus moderately small, elongate, subequal in size to maxillary palpus. Salivary lips well developed, projecting, forming a transverse slit that is wider than that of *Exomalopsis,* about as wide as that of such eucerines as *Tetralonia* and *Eucera,* but narrower than that of such New World eucerines as *Svastra, Melissodes, Xenoglossa,* and *Peponapis.* Hypopharynx normal in size, strongly bilobed with lobes separated by moderately wide longitudinal cleavage; hypopharynx exceeded by labiomaxillary region; integument with conspicuous spicules over much of lobes; hypopharyngeal groove moderately deeply impressed.

BODY: Integument without setae (or if present, setae are so small as to be nearly invis-

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[3] We follow here the anatomical terms proposed by Rozen and McGinley (1974) for the mandibular areas since the names are broadly applicable to bee larvae. In the description of the mandible of *Exomalopsis chionura* (Rozen, 1957), the term "cusp" should be replaced with "dorsal apical edge."
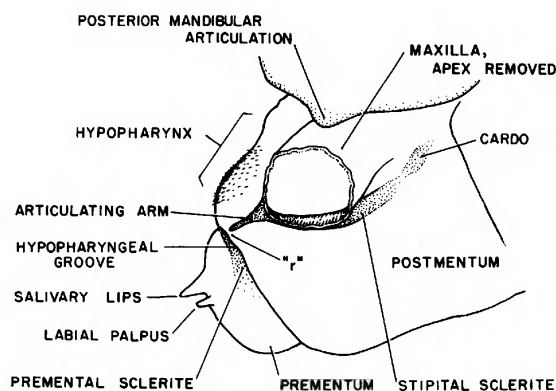
Fig. 12. Mature larva of *Paratetrapedia swainsonae*. Labiomaxillary region with mandible and apex of maxilla removed, lateral view. For explanation, see text.

ible); integument nonspiculate except for conspicuous patches of spicules on lateral part of each dorsal body tubercle and for inconspicuous patches on ventral regions including abdominal segment IX; body without conspicuous spines or sclerotized tubercles. Body form (fig. 4) moderately elongate; intersegmental lines moderately incised; intrasegmental lines scarcely evident; paired dorsal tubercles present as moderately low, distinct, somewhat transverse elevations on thoracic segments and on caudal annulets of most abdominal segments; lateral abdominal tubercles and ventral lateral tubercles virtually absent; venter of abdominal segment IX produced as in *Exomalopsis* (and as in *Paratetrapedia gigantea,* Oliveira, 1962); abdominal segment X moderate in length, rounded in lateral view, attached to upper part of segment IX as in *Exomalopsis*; dorsal surface of segment X with inconspicuous transverse ridge; venter of segment X slightly protuberant in contrast to dorsal part of segment; anus positioned somewhat dorsally on segment X. Spiracles (fig. 10) moderately small, without spiracular sclerites, and nearly identical to those of *Exomalopsis* (and *P. gigantea,* Oliveira, 1962); peritreme flat to slightly concave; spiracular atrium projecting above body wall, globose and without spines or other ornamentation; primary tracheal opening with collar; subatrium of approximately nine chambers, moderate in length. Male with transverse cuticular scar on posterior part of

abdominal venter IX; female characteristics unknown.

MATERIAL STUDIED: Two postdefecating larvae, Bermuda Road near Irish Town, St. Andrew Parish, Jamaica, W.I., June 3, 1985, C. D. Michener.

REMARKS

The description above incorporates a number of anatomical terms and concepts not used previously. They result from an analysis of the anatomical boundaries and sclerites associated with the hypopharynx, maxillae, and labium of this bee and are applicable to larvae of many other bees and perhaps to other Hymenoptera larvae. We refer to the works of Michener (1953), Short (1952), and Snodgrass (1935) in the following discussion:

MAXILLA: The maxilla of the postdefecating larva of *Paratetrapedia,* as in most other bee larvae, is primarily membranous. Although the cardo is only faintly sclerotic, the narrow sclerite leading anteriorly from it is more conspicuous and is produced internally as a ridge. Called the "labio-maxillary rod" by Michener, it was more appropriately termed the "stipital sclerite" (fig. 12) by Short. It marks the boundary between the fused basal part of the maxilla and the labium, and curves upward where the maxillary apex separates from the labium. At this anterior point it branches, sending forward an arm that extends to the premental sclerite. This arm, present in most if not all larval bees that spin cocoons, seems to articulate at its apex with the premental sclerite in *Paratetrapedia* and in many other bees. However, in some taxa it fuses with the premental sclerite. The articulation is presumably the point identified as *r* in parasitic Hymenoptera by Snodgrass. A groove, perhaps accompanied by an integumental thickening (such a thickening is clearly visible in *Peponapis*), extends between the anterior tips of the articulating arms of the stipital sclerites, thus forming the hypopharyngeal groove of this and most other bee larvae. Dorsal to where the arm branches, the stipital sclerite extends upward and backward as a recurved arm for a short distance alongside the hypopharynx before it disappears. This extension is more pronounced in

some bees than in *Paratetrapedia*. It may be related to the basal plates on the lateral walls of the hypopharynx (*w* as identified by Snodgrass), to the hypopharyngeal sclerite (suspensoria), or to the insertion point of the cranial flexor of the lacinia. Whatever the homologies of the continuation of the stipital sclerite, its articulating arm is an important anatomical feature of bee larvae and can serve as a landmark since it is identifiable in almost all cocoon-spinning larvae examined (with the exception of *Dufourea*). It is generally absent in larvae that have the labiomaxillary region greatly recessed and fused (e.g., most panurgines, *Protoxaea,* most Nomadinae).

LABIUM: The division of the labium into a basal membranous postmentum and a mostly membranous prementum has been recognized by all authorities. The sclerotized part of the prementum has been identified by Snodgrass as the premental sclerite (and by Short as the labial sclerite). In most bee larvae it is greatly reduced if not completely lost, and in *Paratetrapedia* only its two dorsal extensions near the two articulating points of the stipital sclerites are in evidence.

Michener recognized that the position of the premental-hypopharyngeal boundary was uncertain because the salivary opening is clearly anterior to the hypopharyngeal groove that traverses the labium-hypopharynx dorsally not only in *Paratetrapedia* but in almost all other bees. Because of the differences in shape and integumental texture between the area in front and behind this groove in so many bee taxa, the best interpretation is that the salivary opening of larval Hymenoptera, probably larval Lepidoptera, and perhaps other Holometabola migrated forward (perhaps in a common ancestor) and indeed is at the apex of the labium and that the hypopharyngeal groove is the correct anatomical demarcation between the labium and the hypopharynx.

HYPOPHARYNX: This structure, defined laterally by the maxilla and anteriorly by the articulating arms of the stipital sclerite in conjunction with the hypopharyngeal groove, is clearly bilobed in *Paratetrapedia* as well as in many other bee larvae, and in the case of *Paratetrapedia* bears numerous setalike spicules on much of its surface.
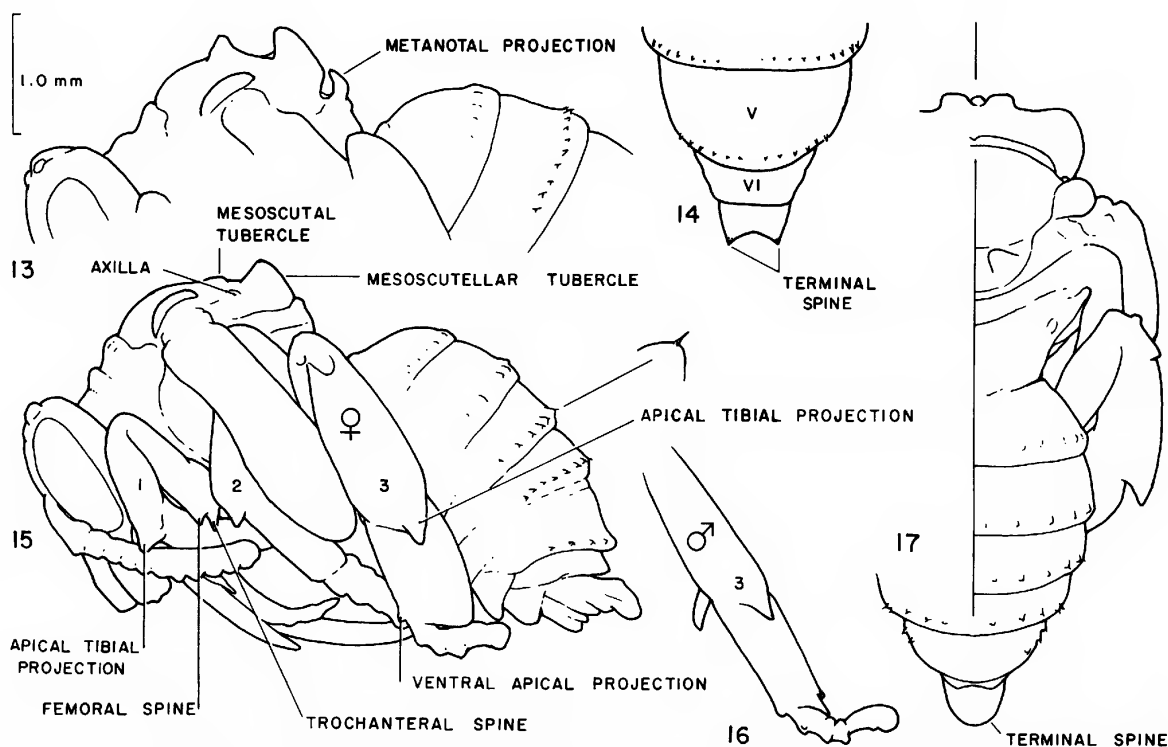
PUPA
Figures 15–17

Because no pupa of the Exomalopsini has been described before, we present the following account. To make the description more meaningful, we parenthetically include contrasting characteristics of *Exomalopsis nitens* Cockerell preserved as a result of a recent study of the nesting biology of the species.

DIAGNOSIS: Although the pupae of *Paratetrapedia swainsonae* and *Exomalopsis nitens* agree on many features, the inconspicuous mesoscutal tubercles and simple, rounded terminal spine of *P. swainsonae* (figs. 15, 17) contrast substantially with the distinct mesoscutal tubercle and sharp pointed, bifurcate terminal spine of *E. nitens* (figs. 13, 14).

HEAD: Integument without setae or spicules. Frons and vertex without tubercles, except for pronounced area immediately mesad of each lateral ocellus which itself is enlarged (in *Exomalopsis nitens,* area immediately mesad of lateral ocellus even more pronounced, projecting farther than ocellus); antenna without tubercles. Gena without spine or tubercle; mandible simple (even though adult mandible bidentate), without ventral tubercle.

MESOSOMA: Integument without setae or spicules. Lateral angle and posterior lobe of pronotum scarcely produced; mesepisternum without tubercles; mesoscutum with pair of very weak tubercles arising from posterior half (these tubercles so weak that they would have gone unnoticed except that in *E. nitens,* distinct moderately small tubercles arise from same area); axilla slightly produced (in *E. nitens,* not produced); mesoscutellum with pair of moderately large tubercles (in *E. nitens,* tubercles more projecting); metanotum with only slight median swelling (in *E. nitens,* with median bifurcate projection); propodeum without tubercles. Tegula nontuberculate; wing without tubercle. Forecoxa with moderate-size apical spine; trochanter with slightly smaller apical spine; femur with ventral basal angle bearing spine; tibia with outer apical projection; basitarsus without apparent modifications. Midcoxa with moderate-size apical spine; trochanter with small apical

Figs. 13–17. Pupae. **13, 14.** *Exomalopsis nitens,* dorsal area, lateral view, and apex of metasoma, dorsal view. **15.** *Paratetrapedia swainsonae,* female, lateral view. **16.** Same, hind tibia and basitarsus of male, lateral view. **17.** Same, right side of female pupa, dorsal view. Scale refers to all figures.

spine; femur with ventral basal angle somewhat less produced than that of forefemur; tibia with conspicuous apical projection. Hind coxa with conspicuous apical tubercle; trochanter with moderately small apical tubercle; femur without conspicuous basal swelling or spine; tibia with conspicuous outer apical spine; basitarsus with inconspicuous apical projection dorsally (somewhat more pronounced in males) and with small but distinct ventral apical projection; tarsomeres 2–3 with very small but distinct apical projections on the ventral inner aspect (these projections particularly noticeable in males, and presumably accommodating developing setae) (apical tubercles on tarsomeres of *E. nitens* apparently far less conspicuous).

METASOMA: Integument without setae. Tergum I with apical row of irregularities too inconspicuous and poorly formed to be called tubercles; tergum II with apical row of low moderate-size tubercles most of which do not bear apical pigmented spicules; terga III–VI (male) and III–V (female) each with apical

row of small but distinct tubercles usually, though not invariably, bearing sharply pointed, pigmented spicules at their apices (in *E. nitens,* apical rows of tubercles with more and longer spicule-bearing tubercles, and tergum II with tubercles usually bearing spicules). Sterna II–IV of female each with moderate-size median posteriorly directed apical projection. Terminal spine short, simple, apically rounded, and not bearing spicules (in *E. nitens,* terminal spine moderate in length, bifurcate, each branch bearing darkly pigmented apical spicule).

MATERIAL STUDIED: Two male, three female pupae, same locality and date as larvae.

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